PROC. BIOL. SOC. WASH.
102(2), 1989, pp. 339–361

A REVISION OF THE GENUS *MICROPROTUS* RICHARDSON WITH DESCRIPTIONS OF TWO NEW SPECIES, *M. ACUTISPINATUS* AND *M. LOBISPINATUS* (ASELLOTA, ISOPODA, CRUSTACEA)

George D. F. Wilson, Oleg G. Kussakin, and Galina S. Vasina

Russian Abstract.—

РЕЗЮМЕ

Ревизия рода Microprotus Richardson с описанием двух новых видов (Asellota, Isopoda, Crustacea)
Уилсон Дж.Д.Ф., Кусакин О.Г., Васина Г.С.

В результате проделанной ревизии рода Microprotus, ранее относимого к примитивному среди Asellota семейству Janiridae, описаны два новых вида из батиали райопа Курильских островов, вид Storthyngura paradoxa Birstein перенесен в этот же род. Показано, что, несмотря на отсутствие плавательных переоподов, род Microprotus должен быть перенесен в одно из наиболее высоко специализированных семейств Asellota—Munnopsidae s.l., для представителей которого характерны плавательные задние пары плеоподов. Приводятся Диагнозы семейства Munnopsidae s.l. в объеме, включающем семейства Eurycopidae, Ilyarachnidae и Munnopsidae s. s., рода Microprotus и всех пяти известных видов этого рода. Обсуждаются родственные связи Microprotus с другими родами Munnopsidae в частности с родом Storthyngura, к которому он наиболее близок, хотя Storthyngura—типичпая Eurycopidae с плавательными переоподами, отсутствующими у Microprotus. Обсуждается вопрос, является ли отсутствие плавательных переоподов у Microprotus плезиоморфным признаком или это—результат вторичного упрощения.

Abstract.—The genus *Microprotus* Richardson, referred earlier to the relatively plesiomorphic family Janiridae, is revised. Two new species from the bathyal zone of the Kurile Islands, *M. acutispinatus* and *M. lobispinatus,* and *Storthyngura paradoxa* Birstein are also placed in this genus. *Microprotus* should be included in the Munnopsidae s.l., in spite of its lack of the highly specialized posterior natatory pereopods that characterize this family. Diagnoses are given for the family Munnopsidae s.l., for the genus *Microprotus,* and for all five species referred to this genus. The relationships between *Microprotus* and other munnopsid genera are discussed, and it is found to be most closely related to *Storthyngura.* Whether the absence of natatory pereopods in *Microprotus* is a plesiomorphic or an apomorphic reversion is discussed; the latter hypothesis is favored.

The status of the janiroidean genus *Microprotus* has been suspect since its inception. Richardson (1910) described two individuals from the South Bering Sea which she put in the family Janiridae, where the genus remained until now. Her remarks on the genus include the statement (Richardson 1910:116) "This genus has affinities with the Munnopsidae" (under Sars' (1899) definition, this family also included *Eurycope* and *Ilyarachna*), but later in the text she writes "The absence of natatory legs, the general form of the body and the style of the uropods, however, are characters referable to the Janiridae." The Munnopsidae Sars s.l. (Wilson 1989) is defined by unique natatory modifications, including paddle-shaped posterior legs with many fringing plumose setae. Richardson's (1910) species, *M. caecus,* closely resembles some species in the munnopsid genus *Storthyngura,* except that its posterior legs are not in the least paddle-shaped and they have no plumose swimming setae.

Vanhöffen (1914), the author of the genus *Storthyngura,* described a new species, *Microprotus antarcticus* from pleotelson fragments. Apparently Vanhöffen did not regard this species as a member of *Storthyngura* and included it in his currently unused and misspelled family Jolellidae. *Storthyngura,* however, has come to include a great variety of forms (see reviews by Birstein 1957, George & Menzies 1968a, b). Birstein (1970) included the species *paradoxa* in *Storthyngura* despite its lack of natatory posterior pereopods. His comments (translated) are revealing: "This inexplicable trait [lack of swimming limbs] contradicts not only the diagnosis of the genus but even that of the family, although in all the other characteristics the new species can be regarded as a typical form of the genus *Storthyngura.*" Birstein (1970) undoubtedly overlooked the obscure genus *Microprotus* because all authors, including Wolff (1962), had put it in the Janiridae.

In this paper, we remove the veil of obscurity from *Microprotus* by providing new descriptions of the its members, and by discussing the meaning of its lack of natatory limbs, at least from a phylogenetic point of view. *M. caecus* is redescribed, two new species are fully described, and diagnoses and a key to all species are provided. We argue that *Microprotus* is a derived member of the Munnopsidae related to the heterogeneous genus *Storthyngura,* and that the absence of natatory limbs is a reversion to a primitive condition, rather than a plesiomorphy.

The Systematic Position of *Microprotus*

We present here a formal diagnosis of the Munnopsidae Sars, 1899 (sensu Wilson 1989), to aid the discussion of the systematic position of *Microprotus.*

Family Munnopsidae Sars, 1899 s.l.

Diagnosis (derived from Wilson, 1989).—Janiroidea with a distinct natasome: pereonites 5–7 enlarged, muscular, with articulations often broadly joined or fused; posterior ventral nerve cord ganglia fused into a single mass in pereonite 5; pleotelson generally tapering posteriorly. Pereopods V–VII natatory (in most genera) with many long, fully plumose setae on margins of broad, paddle-like carpi and propodi. Pereopodal dactylar claws with trough-like hollow between superior and inferior claws enclosing distal sensillae. Antennular article 1 broadened and laterally flattened.

Discussion.—The above definition of the Munnopsidae subsumes the smaller families Eurycopidae, Ilyarachnidae, and Munnopsidae s.s. The diagnosis includes features that are found in no other family of the Janiroidea in this combination. For a more detailed discussion, see Wilson 1989). The best corroborated phylogenetic trees of the Munnopsidae (Wilson 1989) suggest that the ancestral munnopsid had the following characters in addition to the diagnostic characters above: rostrum (a distinct frontal projection between the antennulae) present, natasomal pereonites and pleotelson freely

articulated, pleopod III rami with many plumose setae.

The diagnosis of the Munnopsidae is presented here because *Microprotus* is a significant exception in its lack of natatory legs (Figs. 3D, 7, 10). This genus nevertheless has all other diagnostic characters including a completely fused natasome, an unusual feature for an ambulatory animal (Fig. 1A–B). Given this distribution of characters, two possible hypotheses emerge for the classification of this genus: (1) the non-natatory legs are plesiomorphic within the Munnopsidae, and *Microprotus* diverged early in the evolution of the family before swimming was acquired, i.e., it is the sister group of the remaining munnopsids; or (2) the non-natatory legs are a complete reversion, are a distinctive autapomorphy for the genus, and other characters must be used to establish the affinities of the genus within the Munnopsidae. Using the non-natatory pereopod character alone, one would be forced to accept hypothesis 1 (*H1*) over hypothesis 2 (*H2*) because the former is more parsimonious. Several other character complexes are examined here to establish which hypothesis is most likely. The parsimony values are counted globally for the Munnopsidae.

Cephalon (Fig. 1E; Wilson 1989, fig. 38): The ancestral munnopsid probably had a distinct rostrum, while *Microprotus* does not. *H1* predicts either that the presence of a rostrum in other munnopsids is a reversion or that *Microprotus* lost the rostrum independently of other munnopsids (two evolutionary steps), while *H2* predicts that only the immediate ancestor of *Microprotus* (and taxa of its clade) lost the rostrum in its evolution (one evolutionary step).

The cephalons of some munnopsids bear a synapomorphy called the frontal ridge, a supporting bridge between the mandibular articulations on both sides of the head. Because *Microprotus* has a frontal ridge, *H1* predicts that the frontal ridge is a synapomorphy of all munnopsids and was subsequently lost in several taxa (e.g., Eurycopinae, Munnopsinae) or was developed at least twice (two steps). *H2,* on the other hand, only requires that the frontal ridge is a synapomorphy of the group to which *Microprotus* belongs (one step).

Table 1.—A parsimony analysis of two evolutionary hypotheses for the non-natatory pereopods V-VII in *Microprotus. H1* = The ancestral munnopsid did not have natapods, and *Microprotus* diverged before natapods were evolved. *H2* = The natapods in *Microprotus* reverted to an ambulatory state. Values are the number of evolutionary steps required in the character for the phylogeny of the Munnopsidae (Wilson, 1989) given that a hypothesis is true.

Character	*H1*	*H2*
Pereopods V–VII not natatory	1	2
Rostrum absent	2	1
Frontal arch present	2	1
Mandibular notch in cephalon	2	1
Natasome completely fused	2	1
Total parsimony values	9	6

In the sister group Acanthaspidiidae and in some munnopsid genera, the mandible articulates with the head by a rounded posterolateral border, while other taxa, including *Microprotus* and *Storthyngura,* have a posterior projection of the mandible that articulates with the cephalon in a narrow posteriorly-directed slot. *H1* suggests that this feature either evolved twice, or evolved once and then was lost in more derived taxa (two steps); *H2* requires only that it is a apomorphy of some group of the munnopsids (one step).

Natasome (Fig. 1A–C): The posterior pereonites and the pleotelson of the ancestral munnopsid, although integrated into a unit, were probably fully articulated because both the Acanthaspidiidae, and several munnopsid genera, such as *Amuletta* Wilson and Thistle, *Munnopsurus* Richardson, and *Munnicope* Menzies & George are fully articulated both ventrally and dorsally. The flexion of the segments, however, is restricted and the integration of the natasome is obvious in these taxa. Because *Microprotus* has a fully fused natasome, *H1* requires that this was achieved independently from the

remaining munnopsids (two steps), while *H2* allows that complete fusion could be a synapomorphy of a subset of the Munnopsidae.

Table 1 shows parsimony values for munnopsid phylogenetic estimates using the characters discussed above under *H1* or *H2*. Although these characters are only a subset of the possible features that are useful in munnopsid systematics (Wilson 1989), they are highly derived features that are unlikely to appear more than once in the evolution of this family. *H1* adds nine steps to the munnopsid phylogenetic tree, while *H2* only adds six steps and is therefore more probable. The ambulatory posterior pereopods of *Microprotus* are best explained as a reversion from a swimming form, and must be an autapomorphy of this genus alone.

Furthermore, the natapod to pereopod reversion is not simply a reduction of features: no natatory landmark is present on pereopods V–VII of the adult (juveniles are unknown at present). There are no natatory setae, the carpi and propodi are much longer than in any other munnopsid, and these segments are tubular rather than flattened. Other taxa, such as *Syneurycope* where the pereopodal swimming function may be greatly reduced, typically retain the remnants of these landmarks (e.g., Haugsness & Hessler 1979, fig. 3I). The detailed similarity between the anterior and posterior legs (Fig. 3B, D) suggests that a genetic transfer in pereopodal developmental processes from anterior to posterior may underlie this reversion (first author's opinion). In the current absence of information on munnopsid genetics, further evidence could be obtained by examining the pre- and postmarsupial development in *Microprotus* species, once juveniles and embryos are collected.

Microprotus Richardson, 1910

Microprotus Richardson, 1910:116.
Storthyngura (pars) Birstein, 1970:352.

Type species.—*Microprotus caecus* Richardson, 1910.

Species included.—*Microprotus caecus* Richardson, 1910; *M. antarcticus* Vanhöffen, 1914; *M. paradoxus* (Birstein, 1970); *M. lobispinatus,* n. sp.; *M. acutispinatus* n. sp.

Diagnosis.—Munnopsidae with ambulatory pereopods V–VII: carpus and propodus elongate and tubular, not flattened, with opposing margins with rows of unequally-bifid setae; all segments lacking plumose swimming setae. Cephalon with frontal ridge and without rostrum. Pereonites 5–7 and pleotelson fully fused, with no free articulations either dorsally or ventrally; natasomal pereonites collectively shorter than ambulosomal pereonites. Body dorsal surface, lateral margins of pereonites and pleotelson, coxae of pereonites 5–7, and basal articles of antenna with elongate spines; pleotelson terminating in pair of elongate spines. Pleotelson with pronounced preanal ridge; ridge and anus not covered by opercular pleopods. Antennular article 1 elongate and subtriangular. Mandible with cuticular projection on posterolateral margin articulating with cephalon in elongate notch. Uropods elongate with tubular protopods and rami.

Additional description.—Body with elongate, anteriorly curved spines in following pattern: dorsal midline with one spine on each pereonite and two on pleotelson; dorsolateral spines on pereonites 2–7; lateral spines on pereonites 5–7; two pairs of spines on lateral margins of pleotelson; one pair of spines on posterior tip of pleotelson; one or two spines on articles 1–3 of antenna; single spines on coxae of pereopods I; paired spines on coxae of pereopods II–IV.

Cephalon without eyes or elongate spines, broader than long, with robust laterally projecting cheeks at mandibular articulation point. Pleotelson broad, in most species broader than long; dorsally trilobed, with central section separated by troughs from dorsally projecting lateral lobes.

Antennular flagellum elongate, with many articles, each article with one or several aesthetascs; articles 2, 3 and 5 near same

length, distinctly longer than article 4; flagellar articles of male very short, wider than long, shorter than article 4. Antenna elongate, length more than two body lengths. Mandible normal but body abbreviated proximal to dorsal condyle and palp; molar process triturative but distally tapering; palp functional, longer than mandibular body; teeth on incisor process not distinct; lacinia mobilis normal with distinct teeth; spine row normal with many spines. Maxillipedal basis with many coupling hooks; epipod elongate, reaching to articulation between palp articles 2 and 3, with small rounded dorsolateral spine.

Pereopod I much smaller than posterior pereopods, with thin carpus and propodus having only simple setae. Pereopods II–VII robust, elongate, with strong unequally-bifid setae on opposing margins of carpus and propodus.

Male pleopod I elongate, much longer than wide, with distinct waist midlength, often with short thick spines or tubercles on ventral surface; distal tip with distinct medial and lateral lobes; lateral lobe more elongate, curving medially posterior to medial lobe. Male pleopod II protopod broad, laterally rounded, distally curving to short pointed tip; protopodal setae on lateral margin short, simple, not hemiplumose; endopodal stylet shorter than protopod length; exopod very short, rounded, with nonprojecting distal hook. Female pleopod II broader than long, without setae on keel. Pleopod III endopod broad and rounded; exopod long, thin, distally rounded; exopod and endopod with numerous plumose setae.

Remarks.—The inclusion of *M. antarcticus* Vanhöffen is rather dubious because the species is known only from fragments. Its pleotelson, however, is more similar to other species of *Microprotus* than to *Storthyngura* so it must remain in this genus until redescribed from new material. We (GSV & OGK) have examined the paratype of *Storthyngura paradox* Birstein (1970): this species has a strong resemblance to *Microprotus* and is transferred herein to this genus. Two new species, *M. lobispinatus* and *M. acutispinatus,* extend the known morphological range of this genus.

Microprotus has clear affinities with the heterogeneous genus *Storthyngura,* which does have well-developed natapods. The two genera share the following characters, often to small details: cephalon shape and mandibular articulation; dorsal and lateral spination; form and orientation of the antennula; uropod shape; fusion of natasomal segments (in some species); shape of venter of pleotelson; pleopod shape. Such a long list of similar features practically guarantees that these two genera form a monophyletic taxon within the Munnopsidae. Formal recognition of this group as a subfamily, however, must wait until the genus *Storthyngura* is revised, and its relationships to *Acanthocope* are clarified.

The subgeneric division of *Storthyngura* provided by George & Menzies (1968b) falls short of being useful because, although they say their analysis was based on 138 characters, only 3 or 4 characters were given in the descriptions of the subgroups; analysis of their groupings is therefore extremely difficult. Furthermore, the subgroups may have dubious meaning because they separate species with truncate or forked pleotelson tips (as in *Microprotus*) into different groups, even though this may be an important character at the generic level. Birstein (1970) also found the classification of George & Menzies (1968b) to be ineffective. *Storthyngura* should be subdivided because the type species *S. elegans* Vanhöffen is flat-bodied and broad while *S. pulchra* Hansen (for example) is deep-bodied and has a muscular natasome. The strongly natatory attributes of the latter species are more like other Munnopsidae, indicating it may have diverged early in the evolution of the *Storthyngura* group. For the moment, *Microprotus* is considered to be among a complex of genera represented by the polyphyletic or paraphyletic genus *Storthyngura.*

Geographic distribution of Microprotus.—This genus is an Indo-Pacific bathyal to upper-abyssal genus with 4 species in the northern Pacific: from 40°N to 52°14′N in the Japan and Kurile-Kamchatka Trenches, and off the South Aleutian Islands. A single Antarctic species has been found in the Davis Sea. This genus inhabits depths in the range of 550–3400 m.

Key to the Species of *Microprotus*

1a. Posterior spines on pleotelson extending to tip of uropods; uropodal exopod distinctly shorter than endopod ..... *Microprotus antarcticus* Vanhöffen, 1914

1b. Posterior spines on pleotelson not extending to tip of uropods; uropodal exopod subequal to endopod 2

2a. Lateral spines on pleotelson broad, nearly as broad as long; male pleopod II stylet not tapering to thin hair-like tip 3

2b. Lateral spines on pleotelson thin, much longer than broad; male pleopod II stylet tapering to thin hair-like tip 4

3a. Dorsal and lateral spines on body distally thick and typically rounded; pleotelson width (excluding spines) distinctly greater than length; male pleopod II stylet long, distinctly longer than half protopod length ..... *Microprotus lobispinatus,* n. sp. (Figs. 5–7)

3b. Dorsal and lateral spines on body distally thin and pointed; pleotelson width (excluding spines) subequal to length; male pleopod II stylet short, distinctly less than half protopod length ..... *Microprotus acutispinatus,* n. sp. (Figs. 8–10)

4a. Dorsal and lateral spines on body strongly denticulate; posterior spines on pleotelson not recurved dorsally; pleotelson dorsal surface without pair of low bumps anterior to uropods; pleotelson width subequal to length ..... *Microprotus paradoxus* (Birstein, 1970)

4b. Dorsal and lateral spines on body finely denticulate; posterior spines on pleotelson strongly recurved dorsally; pleotelson dorsal surface with pair of low bumps anterior to uropods; pleotelson width greater than length ..... *Microprotus caecus* Richardson, 1910 (Figs. 1–4)

The Species of *Microprotus*

Microprotus caecus Richardson, 1910
Figs. 1–4

Types.—Holotype copulatory male, pleotelson damaged, some legs missing, others loose in vial, body length 12.0 mm, USNM (United States National Museum no.) 39521. Paratype copulatory male, damaged, partly dissected, some limbs missing, estimated length 11.2 mm, USNM 39917.

Type locality.—*Albatross* station 4781, 52°14.5′N, 174°13′E, off Cape Sabak, Agattu Island, Aleutian Archipelago, depth 544 m, bottom consisting of fine gray sand and pebbles.

Diagnosis.—Cephalon width 1.1 times pereonite 1 width. Dorsal and lateral spines on body distinctly pointed distally, not rounded, finely denticulate. Pleotelson width 1.3 times length; dorsal surface with pair of low bumps anterior to uropods; lateral spines narrow, length 2.8 times basal width. Male pleopod II stylet short, length 0.45 of protopod length, with curved hair-like distal part. Uropods much longer than posterior spines of pleotelson; endopod length subequal to exopod length.

Additional description of males.—Body (Fig. 1A–D): Cuticle heavily calcified. Preservation color white. All margins and spines rugose, with many fine denticles. Body widest at pereonite 5, body length 2.7 times

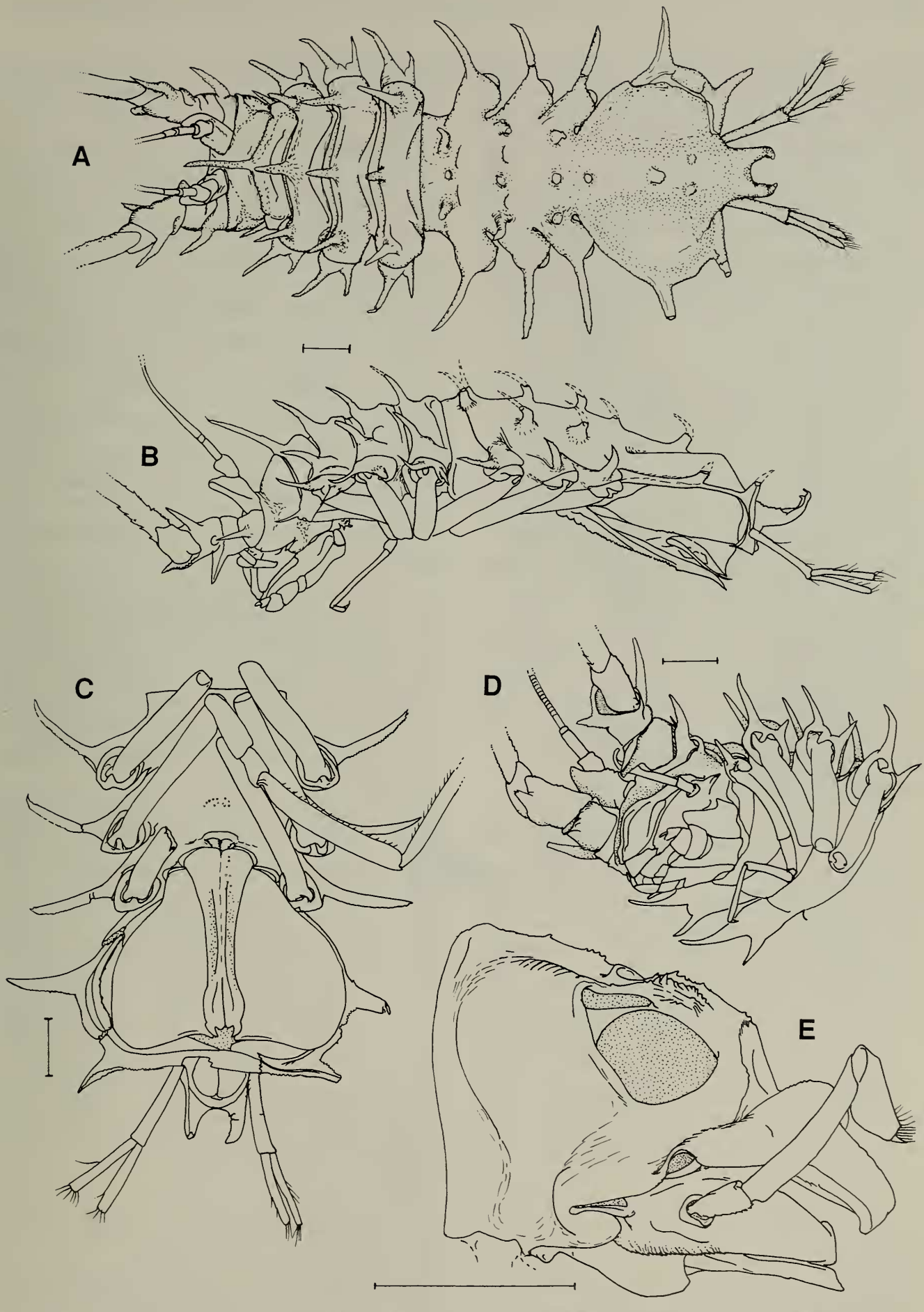


Fig. 1. *Microprotus caecus,* holotype male: A–B, Dorsal and lateral views of body; C, Ventral view of natasome; D, Ventral oblique view of cephalon and ambulosome, pereopods on right side omitted. Paratype male: E, Lateral oblique view of cephalon. Scale bars: 1.0 mm, all.

width. Articular margins of anterior pereonites set in shallow transverse grooves. Dorsal-most parts of pereonites 1–4 also with shallow transverse groove. Pleotelson with pair of short broad spines or bumps posterior to last median spine; bumps not visible in lateral view; lateral spines on pleotelson flattened dorsoventrally, posterolateral spines anterior to uropods triangular in cross-section; posterior spines strongly curving dorsally.

Antennula (Fig. 2H, I): Left antennula of holotype approximately 10 mm long; length 0.83 of body length. Surface of articles 1 and 2 denticulate. Article 1 length 1.9 times width; medial margin with dense group of denticles adjacent to insertion of article 2; dense patch of broom setae proximal to group of denticles on medial margin. Article 2 length 0.39 of article 1 length (including distal lobe). Article 3 subequal to article 2.

Antenna (Fig. 2H): Length 2.8 times body length. Articles 2 and 3 with broad flattened spines projecting ventrally. Article 3 with spine in approximate position of scale. Articles 5 and 6 subequal, length of either 0.22 of total antennal length.

Left mandible (Fig. 2A–D): Incisor process with one distinct cusp ventrally, with remaining incisive margin sinuous and lacking distinct cusps. Lacinia mobilis with four cusps, decreasing in length dorsally; ventral surface of lacinia mobilis with tuft of spinules or cuticular hairs. Spine row with 15 members, distal spines with spinules or cuticular hairs on basal ventral surface. Molar process tapering distally, distal width roughly half proximal width; posterior margin of triturative surface with 8 doubly setulose setae and row of basal denticles, ventral tooth present.

Maxillula (Fig. 2E): Outer lobe with 12 large spine-like toothed setae. Inner lobe distal tip broadly rounded, not extending beyond medial end of outer lobe setal row.

Maxilliped (Fig. 2G): Epipod length 0.93 of basis length; width 0.37 of length; distally rounded. Basal endite with 13 coupling hooks and approximately 5 apical fan setae distally. Palp article 2 width subequal endite width.

Pereopods (Fig. 3A–E): Total length increasing posteriorly with pereopod I disproportionately smaller than others: pereopod I approximately half body length while pereopods II–VI increasing from slightly less (approximately 5% shorter) to near body length. Pereopodal bases: II–IV length subequal; I length 0.71 length of II; V–VII longer than II–IV, increasing in length posteriorly, length ratios with II–IV 1.1, 1.3, 1.5. Ischia of all pereopods distinctly shorter than corresponding bases: ischia I and VI less than half bases length, ischium II length 0.69 of basis II length. Pereopod I propodus with many fine, blunt-tipped, aesthetasc-like setae; opposing margins of propodus and carpus with only fine setae. Setae of pereopods II–VI: single row of unequally-bifid setae on opposing margins of propodus and carpus; propodus with numerous fine setae both dorsally and ventrally. Superior dactylar claws II–VI with triangular or blunt projection on posterior margin. (Pereopod VII not known.)

Male pleopod I (Fig. 4A–E): Sympod widest at proximal insertion, tapering to less than half proximal width at midlength, and expanding to 0.75 of proximal width distally. Sympod with two broad irregular rows of low spines or bumps on ventral surface. Distal tip of in situ sympod resting exactly at tip of pleopod II protopod. Lateral lobes elongate, pointed, proximally broad, distal parts curving medially. Medial lobes short, rounded, approximately 0.25 of lateral lobe length, with numerous long curved simple setae reaching to tip of lateral lobe on distal margin.

Male pleopod II (Fig. 4F, G): Protopod broad, laterally rounded, with fringe of simple setae laterally and distally; length 1.4 times width; ventral surface with concavity lateral to internal musculature for exopod. Endopod inserting 0.65 of protopod length from pleopod insertion; exopod short, distal

Fig. 2. *Microprotus caecus,* paratype male, mouthparts: A–D, Left mandible: A, Mandible, dorsal view; B, Incisor process and lacinia mobilis, anterior view; C, Molar process, anteromedial view; D, Distal part of mandible showing spine row; E, Right maxillula, ventral view; F, Right maxilla, ventral view; G, Right maxilliped, ventral view. Holotype male: H, Cephalon, dorsal view, showing antennula and antenna; I, Antennular basal articles, in situ. Scale bars: 0.2 mm, all except for H, 2.0 mm long.

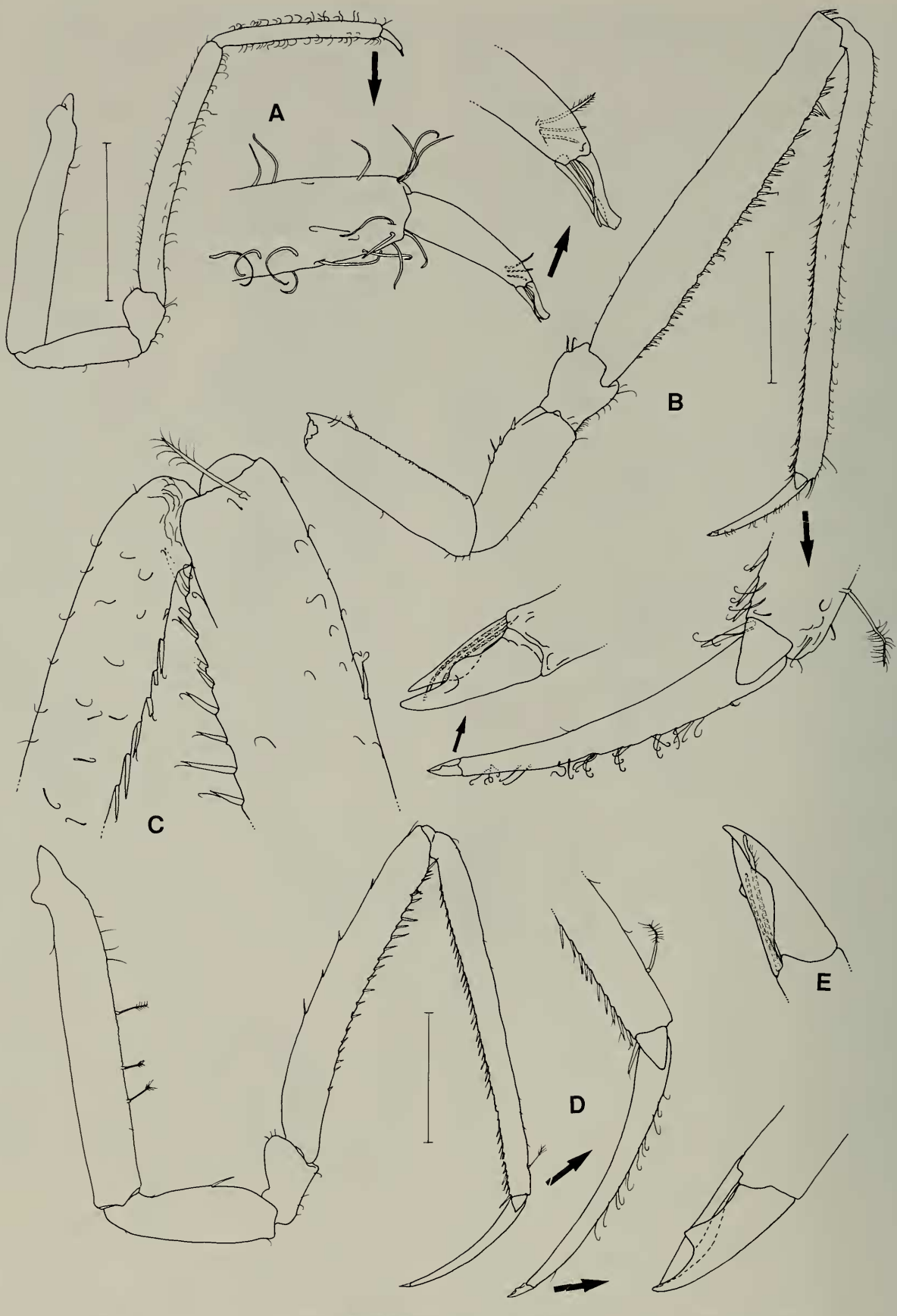


Fig. 3. *Microprotus caecus,* paratype male, pereopods: A, Pereopod I, lateral view; B, Pereopod II, lateral view; C, Enlargement of adjacent parts of carpus and propodus of pereopod VI; D, Pereopod VI, medial view; E, Pereopod VI, enlargement of dactylar claw, lateral view. Scale bars: 1.0 mm.

hook not protruding, with small distal tuft of fine simple setae; exopodal extrinsic musculature small compared to size of protopod, extending only half way to lateral margin of protopod.

Pleopod III: Exopod distally rounded, with approximately 17 plumose setae. Endopod distally broad, rounded, very thin, fringed with numerous setae.

Uropod (Fig. 4H): Long, thin, with short setae, length 0.69 of pleotelson length. Endopod and exopod subequal, length of either 0.87 of protopod length.

Remarks.—*Microprotus caecus* is known only from two adult male specimens; females or juveniles have not been collected. This species may be distinguished from other species of the genus by the following characters: cephalon only slightly wider than pereonite 1; spines distinctly pointed, not rounded distally; pleotelson much wider than long; lateral pleotelson spines that are much longer than their basal width; and subequal uropodal rami. Overall, the other species are similar to *M. caecus,* perhaps with the exception of *M. antarcticus* whose pleotelson shape differs rather more.

Richardson (1910: fig. 38) illustrated the holotype of *Microprotus caecus* with distinct articulations between the natasomal segments. Study of the type material reveals that the natasome is fully fused with no free articulations. The dorsal surface of the natasome, however, does have slight ridges that are either remnants of the articulations or exterior expressions of apodemes. These ridges further corroborate the contention that pereonites 5–7 are natasomal in origin because each ridge extends well into the segment anterior to it (Fig. 1A), as is typical with most munnopsids.

Microprotus lobispinatus, new species
Figs. 5–7

Types.—Holotype male, 12 mm long, (Zoologicheskogo Instituta Akademiya NAUK (ZIN) No. 1/81502). Paratype male, 11 mm, (ZIN No. 2/81503).

Type locality.—Pacific Ocean, near Iturup Island, 44°52′N, 149°27′E, depth 910–920 m, habitat: muddy sand with stones, 25 Jul 1984, coll. B. Sirenko.

Diagnosis.—Dorsal and lateral spines on body thick and rounded distally; spines finely denticulate. Pleotelson width (excluding spines) 1.2 times length; lateral spines broad, length subequal to basal width. Male pleopod II stylet 0.66 of protopod length, without curved hair-like distal part. Uropods much longer than posterior spines of pleotelson; endopod length subequal to exopod length.

Additional description of adult male (Fig. 5).—Body somewhat robust, front half subequal in width to natasome. Body length approximately 2.2 times body width without lateral spines; body widest at pereonite 4. All dorsal spines distinctly flattened, often with concave front surface, usually curved forwards, sometimes widened in middle part. All dorsal spines with finely spinulous, rasp-like surface.

Cephalon broad, approximately three times wider than long; frontal margin broadly concave.

Pereonite 1 considerably narrower than cephalon, with single medial spine only. Pereonite 2 approximately 1.5 times wider than pereonite 1, slightly wider than pereonite 4 and slightly narrower than pereonite 3. Dorsal surface of pereonites 2–7 with three spines. Medial spines gradually decreasing in length from pereonite 2 to 6, medial spine on pereonite 7 longer than that on pereonite 6. Dorsolateral spines nearly as long as medial spines; on natasomal pereonites, much nearer to medial spines than on pereonites 2–4. Lateral margins of pereonites 1 and 4 rounded, pereonites 2 and 3 nearly truncate, with produced posterolateral angles. Coxal plates of pereonites 2–4 long, strongly produced, each plate with long spine-like lobes, anterior lobe longer than posterior. Coxal

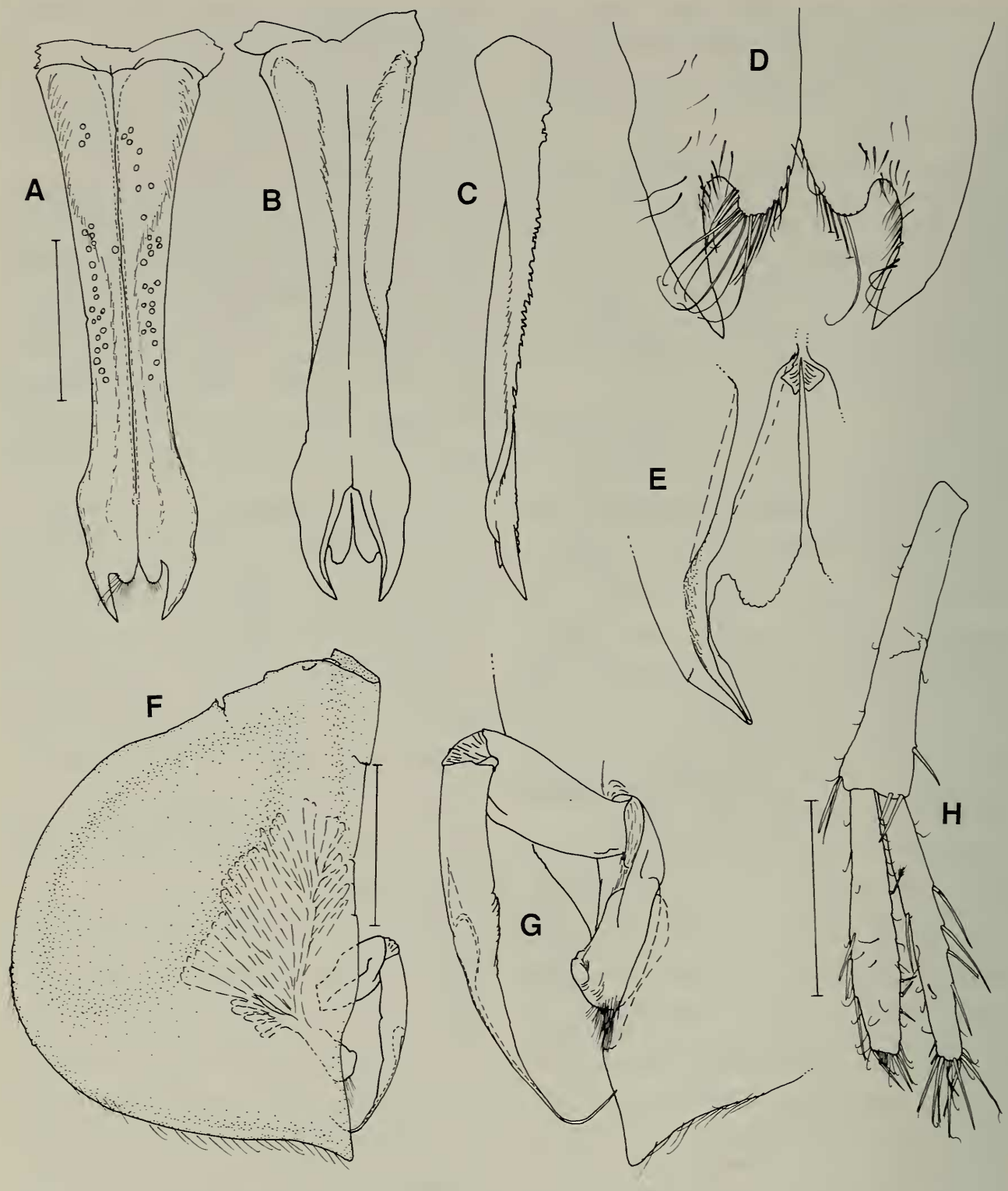


Fig. 4. *Microprotus caecus,* paratype male, pleopods: A–C, Pleopod I, ventral, dorsal, and lateral views respectively; D, E, Enlargements of pleopod I distal tip, ventral and dorsal views respectively; F, G, Right pleopod II, ventral and enlarged dorsal view respectively. Holotype male: H, Left uropod, in situ ventral view. Scale bars: 1.0 mm.

plates of pereonite 1 with single anterior spine-like lobe.

Segments of natasome fused medially but distinct on lateral parts. Anterolateral angles of pereonites 5–7 produced outwards into stout conical spine-like processes. Coxal plates of pereonites 5–7 small, with rounded posterolateral angles.

Pleon length not including posterior spines 0.3 of total body length. Anterodorsal margin of first pleonite slightly marked by shallow transverse depression, posterior margin somewhat more distinct. Dorsal surface of anterior pleonite convex, with median spine strongly curved forwards. Pleotelson broad, 1.3 times wider than long; lateral margins each with two long stout conical spines; anterior spine thicker, located nearly at midlength of pleotelson lateral margin. Dorsal surface of pleotelson with flattened spoon-like median spine curving forwards.

Antennula (Figs. 5, 6F) when bent backwards slightly exceeding middle of body; basal article more than two times longer than broad, its outer margin irregularly convex, inner margin roughly concave; second article inserting near midlength of first article, approximately one third as long as first article, slightly increasing in width distally. Antennal second article with two curved spines, one spine directed outwards, and second inwards. Third article also with two spines, outer spine longer than inner one.

Left mandible (Fig. 6C): Incisor process with one tooth. Lacinia mobilis with two teeth. Spine row with 12 spines, posterior spines longer than anterior ones. Molar process forming truncate cone, cut off distally, with small tooth on inner side and shallow apical excavation in middle. Third article of mandibular palp broad, oval, twisted, with numerous marginal setae, longer than palp article 1.

Maxilliped (Fig. 6A, B): Endite with 10 coupling hooks. Epipod approximately three times longer than broad, distally rounded, with triangular lateral projection.

Pereopods (Fig. 7A, E, F): Pereopod I simple, little differentiated; carpus approximately 2 times longer than propodus; both articles with numerous short setae. Carpus 1.3 times longer than ischium and merus together. Propodus of pereopod II slightly longer than carpus, ventral margin with dense row of bifid spine-like setae, dorsal margin with numerous fine setae; merus

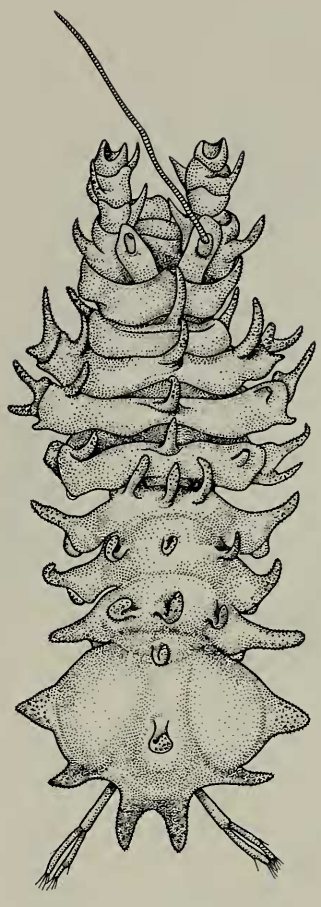


Fig. 5. *Microprotus lobispinatus,* male holotype, body in dorsal view.

short, bearing setae on both margins. Carpus and propodus of pereopods II–VII oblong, narrow, subequal in length, ventral margins with dense row of short spine-like bifid setae; on propodus all setae subequally long, on carpus small setae alternate with larger setae (not shown in Fig. 7E, F); propodus with one distal plumose seta. Pereopod VI propodus slightly longer and nearly twice as narrow as carpus.

Male pleopod I (Fig. 7B): Pair complex narrowest at midlength, length 2.8 times proximal width. Lateral lobe longer than medial lobe, curving medially; medial lobe with distal tip rounded, lobe-like, bearing numerous setae.

Male pleopod II (Fig. 7C): Somewhat broad; protopod suboval, length nearly 2 times width, inner distal tip triangular, pointed; distal part of outer margin and posterior margin with setae. As compared with *M. acutispinatus,* endopod relatively long.

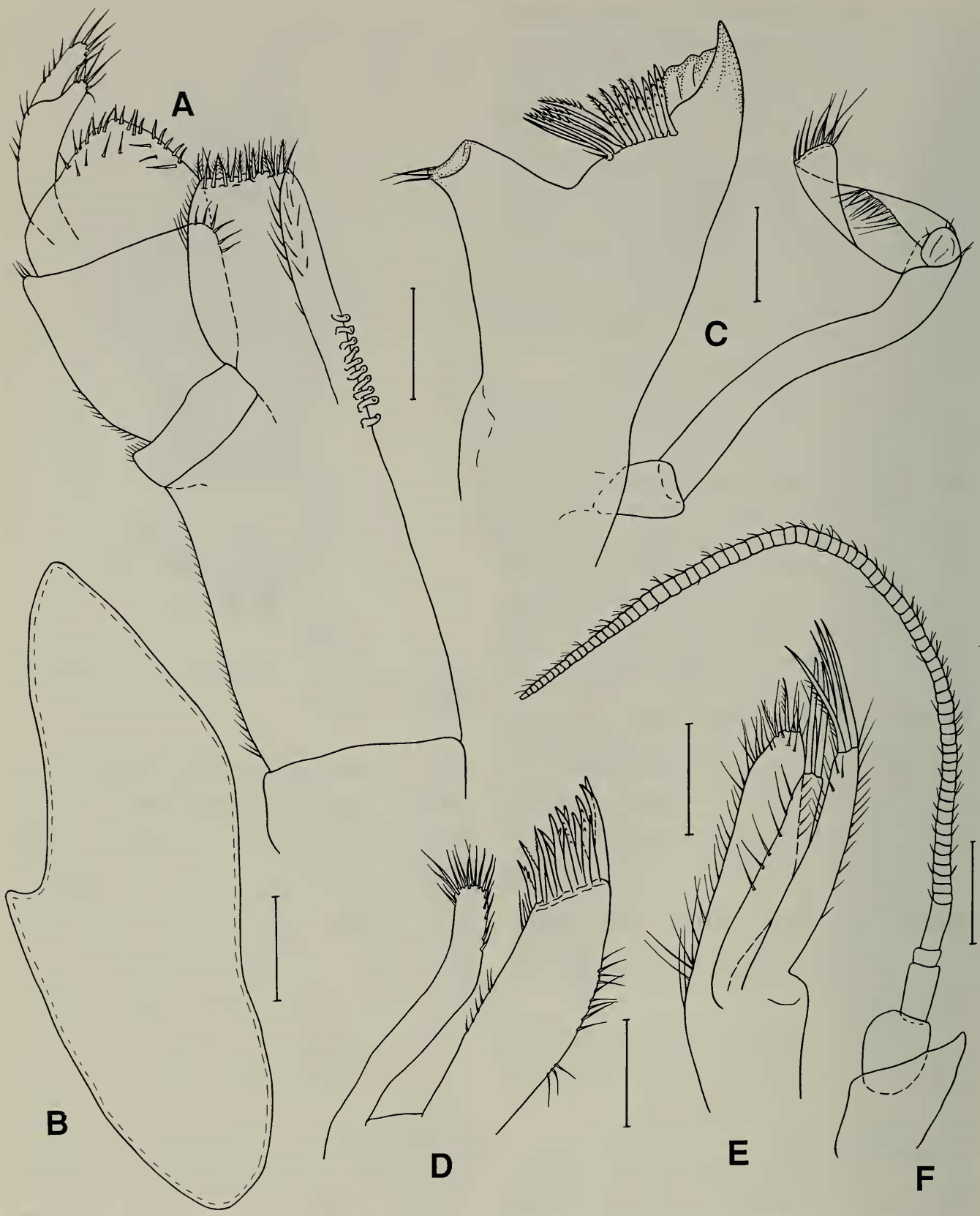
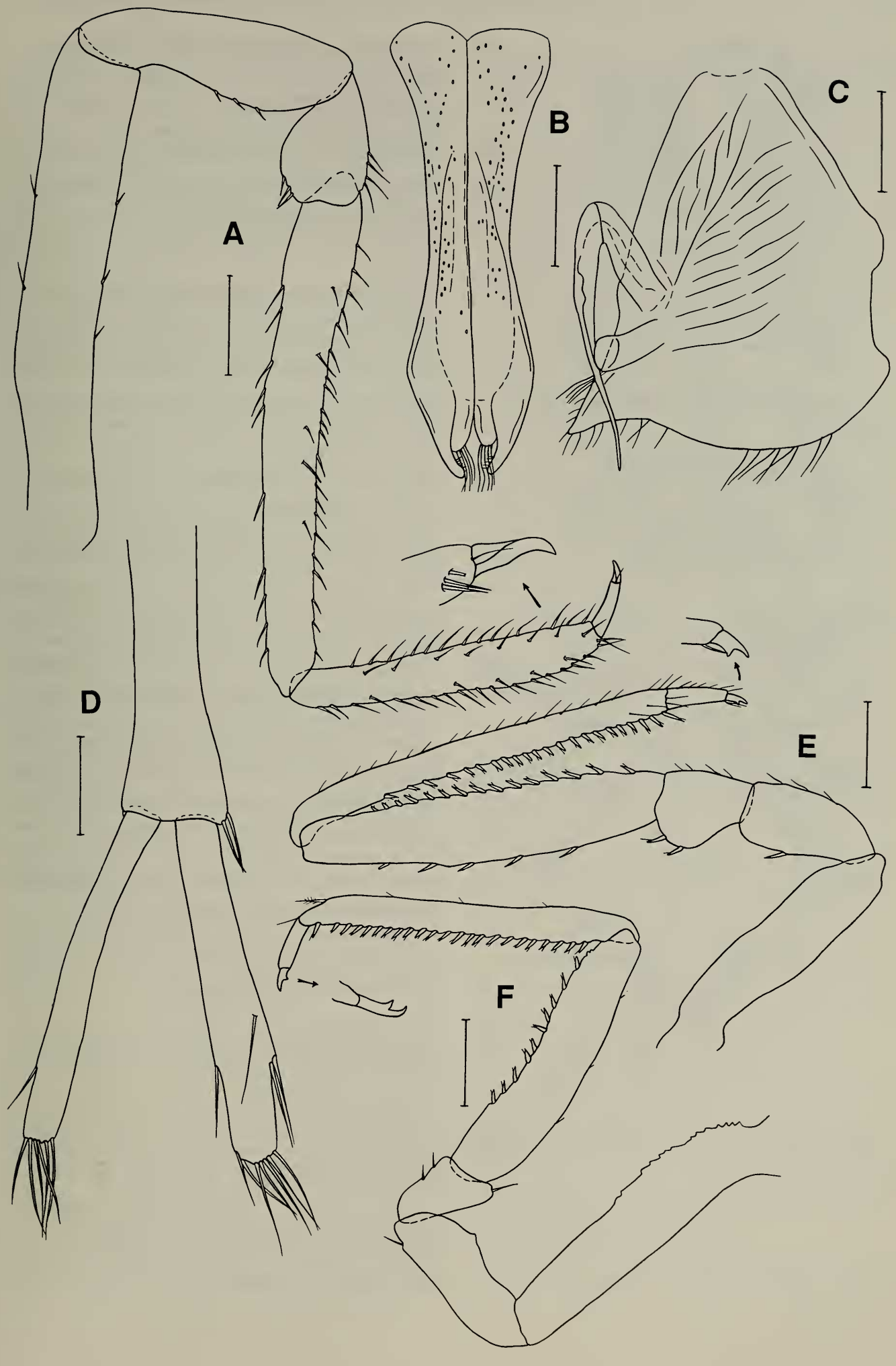


Fig. 6. *Microprotus lobispinatus,* male holotype, mouthparts and antennula: A, Maxilliped, dorsal view; B, Maxillipedal epipod, dorsal view; C, Right mandible, dorsal view; D, Maxillula, ventral view; E, Maxilla, ventral view; F, Antennula. Scale bars: 0.2 mm, all except F, 0.3 mm.

→

Fig. 7. *Microprotus lobispinatus,* male holotype, pereopods and uropod: A, Pereopod I; B, Pleopod I; C, Pleopod II; D, Uropod; E, Pereopod II; F, Pereopod VII. Scale bars: 0.2 mm—B–D; 0.3 mm—A; 0.5 mm—E, F.


A
B
C
D
E
F

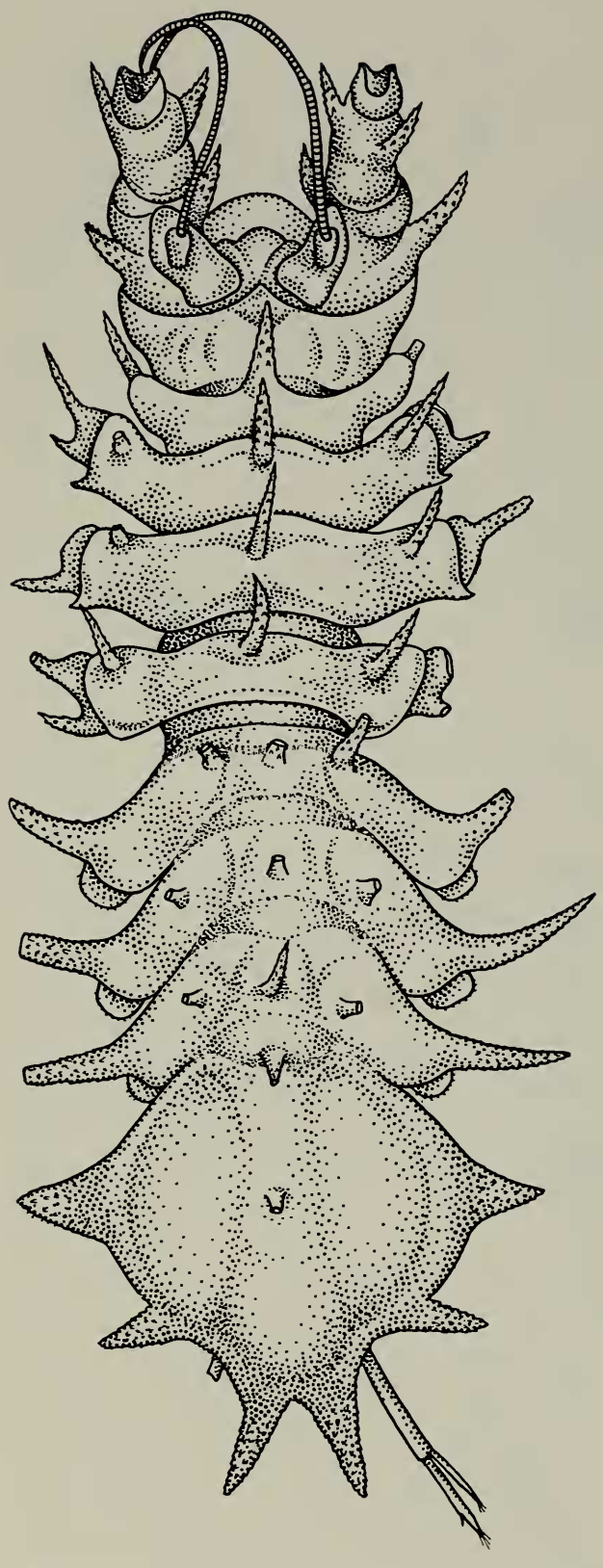


Fig. 8. *Microprotus acutispinatus,* male holotype, body in dorsal view.

Stylet extending slightly beyond distal tip of protopod, length 0.7 of total protopod length. Exopod small, with dense group of fine simple setae on posterior curve.

Uropod (Fig. 7D): Very long and slender, extending much beyond posterior spines of pleotelson. Endopod slightly shorter than exopod; latter ramus nearly as long as protopod.

Remarks.—*Microprotus lobispinatus* is represented by only two adult males from one sample. This species can be distinguished from all Pacific species by the wide, apically flattened and rounded dorsal spines. *M. lobispinatus* also differs distinctly from *M. acutispinatus* and *M. paradoxus* by its relatively wider pleotelson; the species is similar in this respect to *M. caecus. M. lobispinatus* is easily distinguished from the latter species by having thicker and shorter lateral spines, especially on the posterior pereonites and the pleotelson, by lacking dorsal lumps on the pleotelson anterior to the uropods, and by uropodal protopods that do not extend beyond the posterior spines of the pleotelson (as in *M. caecus*). This new species, like all other boreal species, distinctly differs from *M. antarcticus,* a single species from the southern hemisphere conventionally assigned to this genus, by posterior spines on the pleotelson considerably shorter than the uropods, and by uropodal rami that are nearly equal in length.

Etymology.—"*Lobispinatus,*" the adjectival form of two classical nouns, means "provided with lobe-spines."

Microprotus acutispinatus, new species
Figs. 8–11

Types.—Holotype, male 13 mm (ZIN No. 1/81500). Paratypes, 2 males, 2 females, all fragmented (ZIN No. 2/81501).

Type locality.—Pacific Ocean, near Iturup Island, 44°48′N, 149°31′E, depth 1100–1200 m; habitat: sand with pebbles; 25 Jul 1984, coll. B. Sirenko.

Diagnosis.—Dorsal and lateral spines on body thin and pointed distally; spines finely denticulate. Pleotelson width (excluding spines) subequal to length; lateral spines broad, length subequal to basal width. Male pleopod II stylet 0.4 protopod length, without curved hair-like distal part. Uropods much longer than posterior spines of pleotelson.

Additional description of adult males (Figs. 8, 11B, E).—Body relatively slender, slightly widening posteriorly, so that natasome distinctly wider than pereonites 1–4 and cephalon; length slightly more than three times body width across pereonite 5 without lateral projections. All dorsal spines rather slender, narrow-conical, pointed, their surfaces covered with minute spinules. Dorsal spines directed forwards and upwards on pereonites and backwards and upwards on pleon.

Cephalon broad, width approximately three times length; frontal margin broadly concave.

Pereonite 1 distinctly narrower than cephalon, with single median dorsal spine. Pereonites each with three spines; median spines subequal in length. Dorsolateral spines on natatory pereonites placed much nearer to medial spines than on pereonites 2–4. Lateral margins of pereonites 1 and 4 rounded, those of pereonites 2 and 3 nearly truncate, posterolateral angles produced outwards. Coxal plates of pereonites 2–4 with two produced, long, spine-like lobes (damaged on pereopod III in Figs. 8, 11A–C); anterior lobe longer than posterior one. Segments of natasome lacking dorsal articulations; pereonites 5–7 and pleon not clearly delimited. Anterolateral corners of pereonites 5–7 produced outwards into stout, conical spine-like projections. Coxal plates of pereonites 5–7 in dorsal view relatively short, suboval in form.

Pleon length excluding posterior spines approximately one third total body length. First pleonite small, narrow, convex dorsally, with medial dorsal spine curved backwards. Pleotelson (without projections) only slightly broader than long, somewhat produced posterior part with pair of long spine-like pointed projections directed backwards and slightly outwards and two pairs of lateral long stout conical spines: anterior spine considerably thicker and slightly longer, located approximately at midlength of lateral margin of pleotelson, posterior spine smaller and placed near posterolateral angle of pleotelson. Low broad dorsomedial keel with recurved spine-like process in middle part.

Antennula (Fig. 8) when bent backwards, reaching midlength of body; basal article two times longer than broad, its outer margin irregularly convex, inner margin concave; second article inserting at midlength of basal article, approximately one third length of basal article, slightly widening distally.

Antennal (Figs. 8, 11B) second article with two stout spines, one on inner and another on outer margin, third article also with two subequal spines.

Left mandible (Fig. 9D): Incisor process with one tooth. Lacinia mobilis with three teeth. Spine row with eight setae, posterior spines longer than anterior ones. Molar process conical, obliquely cut off distally, with four setae on distal posterior edge; distal triturating surface with conical tooth. Third article of mandibular palp longer than first, broad, twisted, with setal row.

Maxilliped (Fig. 9A): Endite with 11 coupling hook on inner margin. Epipod three times longer than broad; distally rounded, with triangular lateral projection.

Pereopod I (Fig. 10C) simple, little differentiated; carpus slender and very long, length 1.4 times ischium and merus length together and 1.6 times propodus length. Ventral and dorsal margins of propodus and ventral margin of carpus with rows of short stout spine-like bifid setae.

Pereopod II (Fig. 10D): Propodus somewhat longer, slightly longer than carpus, with

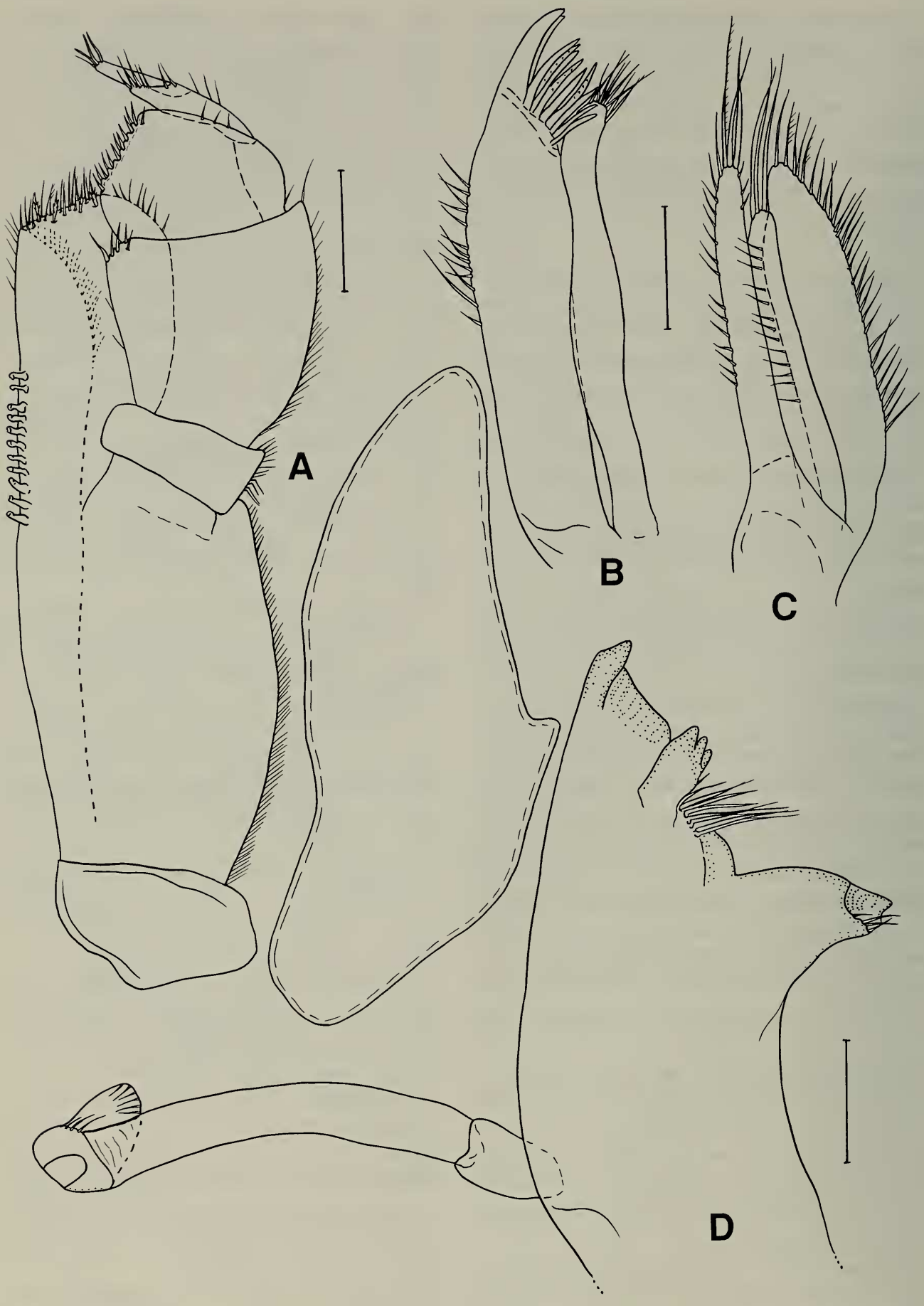


Fig. 9. *Microprotus acutispinatus,* male holotype, mouthparts: A, Maxilliped and epipod, ventral view; B, Maxillula, ventral view; C, Maxilla, ventral view; D, Left mandible, dorsal view. Scale bars: 0.2 mm.

setae only along ventral margin. Carpus with four bifid setae on ventral margin. Dorsal margin of merus serrate distally.

Pereopods V–VII (Fig. 10E): Carpus and propodus long, slender, linear, subequal in length, without natatory setae, but ventral margins with row of short stout spine-like bifid setae. Dactylus short.

Male pleopod I (Fig. 10A): Pair complex much narrower in middle part; length approximately 2.5 times proximal width. Lateral lobe much longer than endopod; distal tip of medial lobe narrowly rounded, with short row of simple setae arranged in fan-like order.

Male pleopod II (Fig. 10B): Protopod very broad, length approximately 1.5 times longer than wide, semicircular, distomedial corner slightly produced, pointed; posterior margin and distal part of outer margin with row of thin simple setae. Endopod and exopod small, reaching well short of distal tip of protopod. Stylet relatively short, extending only slightly beyond distal margin of exopod and not reaching tip of protopod. Exopod with dense group of long, fine, simple setae on posterolateral margin.

Uropods (Fig. 8) long and slender, extending beyond posterior spines of pleotelson. Exopod slightly shorter than endopod; latter nearly as long as protopod.

Description of female.—In general, outline (Fig. 11A, C, D, F) similar to male; body length 12 mm. Dorsum somewhat wider than in male. Pleotelson bearing two tiny low lumps posterior to central dorsal median spine and anterior to uropods, similar to those in *M. caecus* (lumps not visible in lateral view, hidden by swelling of dorsal surface of pleotelson lateral to depressed medial part). Pleopod II (Fig. 10G) very broad, 1.3 times broader than long, ventromedial keel without setae.

Remarks.—*Microprotus acutispinatus* is represented by five specimens: three adult males and two females, of which only the holotype male is preserved in relatively good condition. The other individuals are badly damaged, their bodies having broken in half. This species is easily distinguished from *M. caecus* and *M. lobispinatus* by its narrow pleotelson, which is nearly as wide as long and similar in this respect to *M. paradoxus*. It differs, however, from the latter species by the narrowly conical (not flattened) dorsal spines on the pleotelson which are considerably shorter and stouter than those of *M. paradoxus*.

Etymology.—"*Acutispinatus,*" containing the adjectival form of "spinus" and modified by "acutus," means "provided with pointed spines."

Microprotus paradoxus (Birstein, 1970)

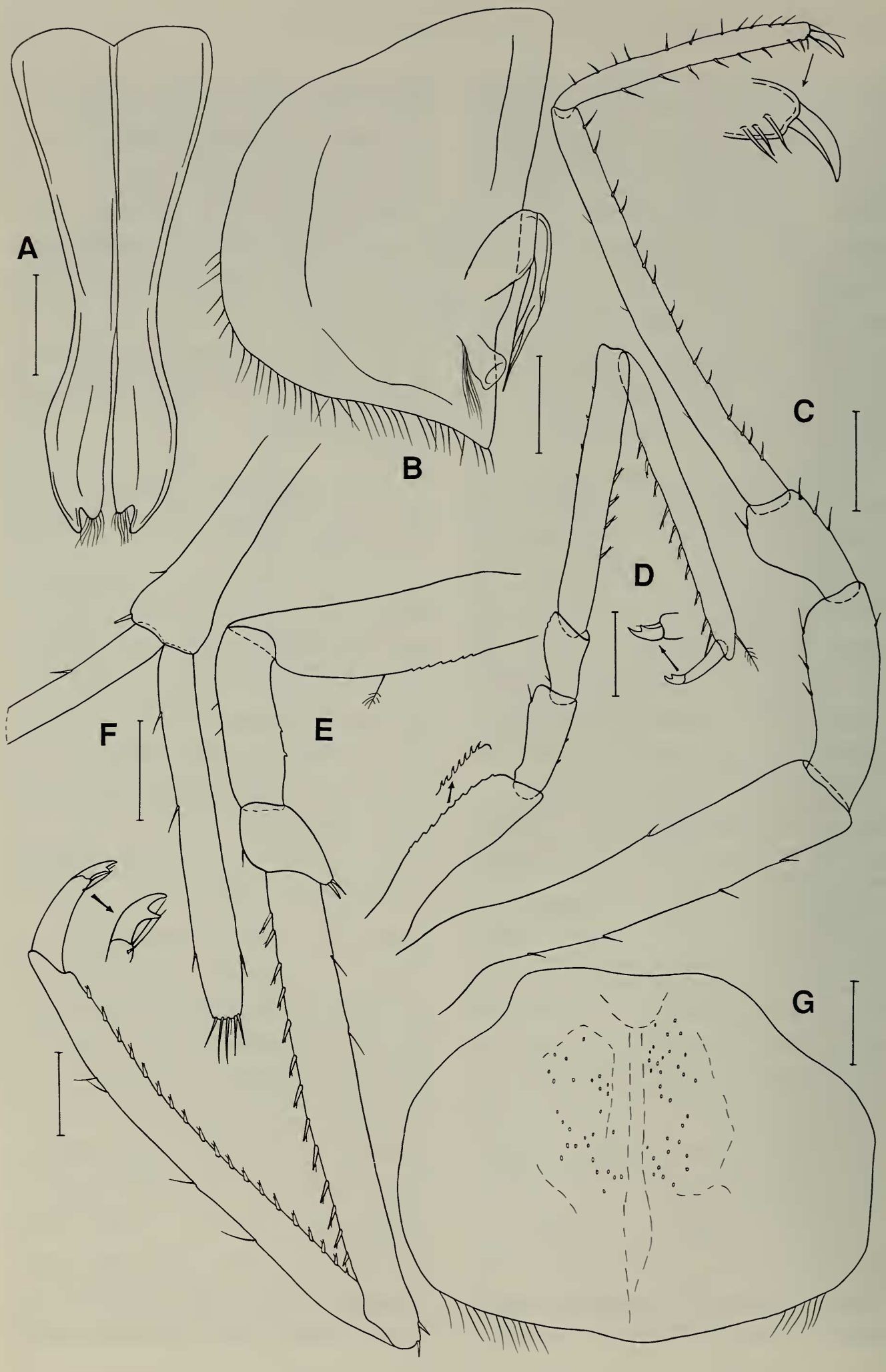
Storthyngura paradoxa Birstein, 1970, p. 334, Figs. 19–20.

Syntypes.—Types were not found by Dr. Mezhov, who looked for them at our request in the deep-sea isopod collection studied by the late Professor Ya. Birstein. The collection was first deposited in the Department of Invertebrate Zoology of Moscow University, was later handed over to the Institute of Oceanology, and finally was deposited in the Zoological Museum of Moscow University.

Type locality.—Kurile-Kamchatka Trench, *Vityaz* Station 5601, 46°26′N, 152°07′E, 2770–2820 m.

Additional material.—Japan Trench, *Vityaz* Station 6671, 40°15′N, 143°35′E, 2500 m. Three adult males (14.8, 14.6, and 12.9 mm long), one male fragment, one damaged female with oostegites (13.8 mm long), two fragments of females. This material was identified by B. Mezhov who kindly showed it to one of the authors (GSV).

Diagnosis.—Dorsal and lateral spines on body thin and pointed distally; spines coarsely denticulate. Pleotelson width (excluding spines) subequal to length; lateral spines narrow, length much greater than width. Male pleopod II stylet short, 0.44 of protopod length, with curved hair-like distal part. Uropods much longer than poste-


A
B
C
D
E
F
G

rior spines of pleotelson; endopod length subequal to exopod length.

Remarks.—The specimens from the Japan Trench in general correspond well to descriptions and drawings of syntypes given by Birstein. This species is clearly distinguished by considerably thinner and longer acute spines on the posterior part of the body; these spines are not bent dorsally and extend far beyond the distal ends of the uropodal protopodites. The dorsal surface of the pleotelson lacks lumps anterior to the uropods and the pleotelson is relatively narrow. This species differs from *M. lobispinatus* and *M. acutispinatus* by considerably longer and thinner spines on the pleotelson, from *M. lobispinatus* by thin dorsal spines, and from *M. acutispinatus* by a flattened body.

Microprotus antarcticus Vanhöffen, 1914

Microprotus antarcticus Vanhöffen, 1914: 545–546, Fig. 71a–d.

Type.—Only a 2 mm long abdomen with a portion of the posterior pereonal segment and a pereopod basis are known. This material (not examined by the authors) is probably at the Berlin State Museum, East Germany, where other Vanhöffen material has been found.

Type locality.—Antarctic Indian Ocean, Davis Sea, *Gauss* station 30.II.1903, 65°27′S, 80°33′E, 3398 m.

Diagnosis.—Lateral and posterolateral spines on pleotelson robust and elongate, posterior spines extending to distal tips of uropods. Uropodal exopod distinctly shorter than endopod.

Remarks.—*Microprotus antarcticus* may actually belong in another genus of the *Storthyngura* complex, but until more specimens are discovered, this species must be retained in *Microprotus.*

With such scarce material at his disposal, Vanhöffen (1914) could not describe this Antarctic species adequately, and could only give comments, comparing the specimen with *M. caecus,* the only species of the genus *Microprotus* known at that time. According to Vanhöffen, Pacific (Arctic in Vanhöffen's term) and Antarctic species differ mostly in that the latter has a low tubercle on the longitudinal thickening of the caudal segment, while in the Antarctic species, the middle spine between both lateral spines looks abrupt. In addition, there are constrictions over the two posterolateral spines, and the uropods are equal in length to the distal spines, with the outer uropodal ramus being only one third of the inner ramus length. In *M. caecus,* all spines are considerably smaller in comparison with the abdomen, so that uropodal rami, which are subequal in length, extend beyond the distal spines. Judging from the rest of the posterior pereonal segment, the lateral spines in *M. antarcticus* are directed backwards, while in *M. caecus,* they are directed forwards and curved, and the dorsal surface of these segments bears spines. The operculum and other pleopods of the female, which are schematically drawn by Vanhöffen in his figure 71d, do not seem useful in his opinion and cannot be used in comparison because the male was known only for the northern species.

Vanhöffen (1914) put the genus *Microprotus* in his family Jolellidae (*sic*), where he also assigned the genera *Jolella* (*sic,* correctly spelled *Iolella* Richardson), *Janthopsis* (*sic,* correctly spelled *Ianthopsis* Beddard), *Acanthaspidia* Stebbing, *Jolanthe* (*sic,* correctly spelled *Iolanthe* Beddard), *Rhac-*

←

Fig. 10. *Microprotus acutispinatus,* male holotype: A, Pleopod I, ventral view; B, Pleopod II, dorsal view; C, Pereopod I; D, Pereopod II; E, Pereopod VII; F, Uropod. Female paratype: G, Pleopod II. Scale bars: 0.2 mm—A, B, F; 0.3 mm—C; 0.5 mm—D, E, G.

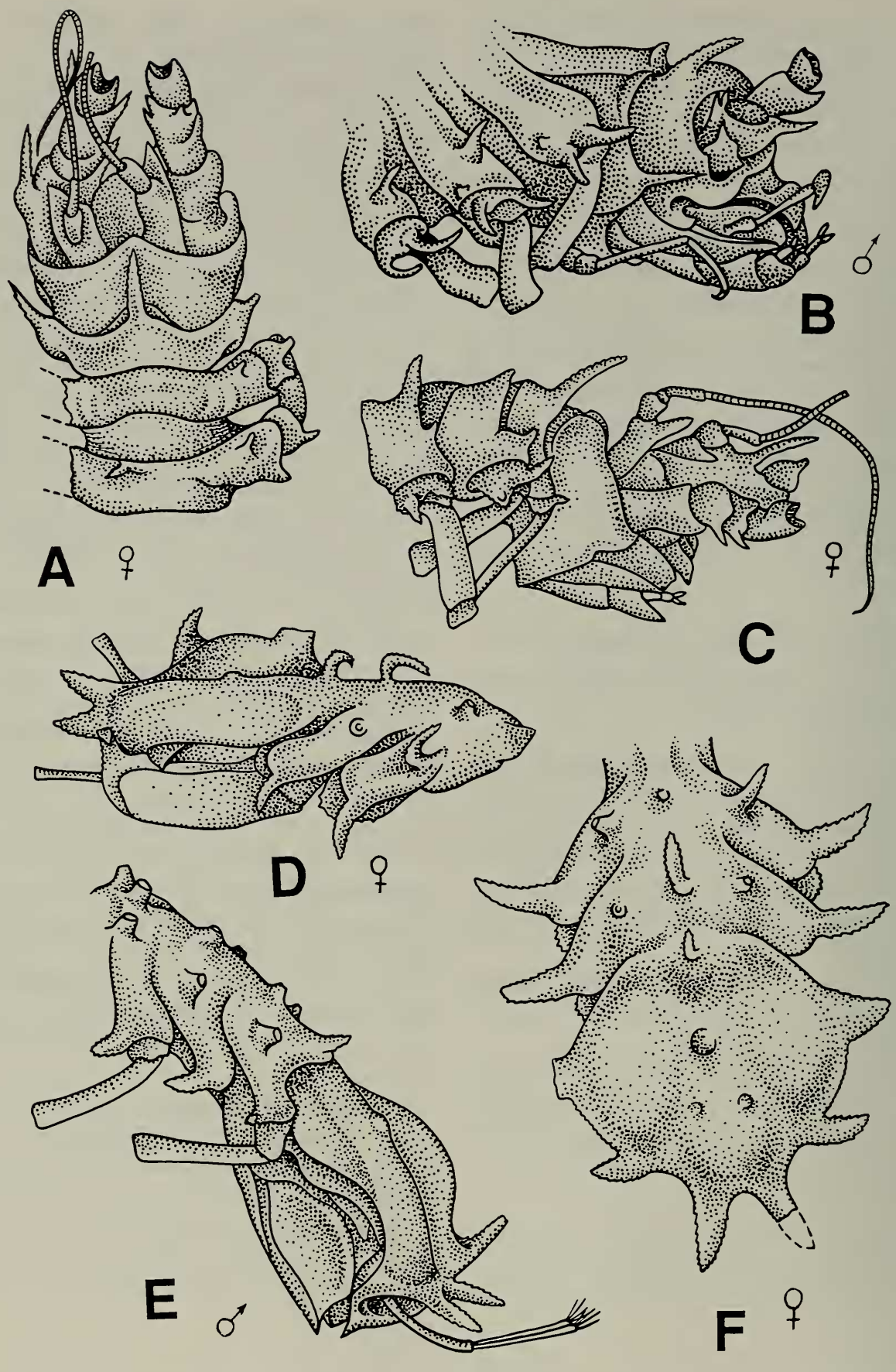


Fig. 11. *Microprotus acutispinatus,* paratypes, body fragments: A, Female, cephalon and pereonites 1–3, dorsal view; B, Male, cephalon and pereonites 1–3, lateral view; C, Female, cephalon and pereonites 1–3, lateral view; D, Female, pleotelson and pereonites 6–7, lateral view; E, Male, pleotelson and pereonites 5–7, lateral view; F, Female, pleotelson and pereonites 6–7, dorsal view.

ura Richardson, and *Jaerella* Richardson. These genera were earlier referred to the family Janiridae, owing to the presence of a more or less distinct rostrum, elongate lateral lobes on the body segments, and two or more lateral spines on the abdomen. In Vanhöffen's opinion, the anterior body part of *Microprotus* is most similar to that of *Iolanthe,* but in the last case, the abdomen lacks distinct distal lobes. At the same time, Vanhöffen noted certain similarities between *Microprotus* and the Munnopsidae, to which he also assigned the Eurycopidae: similar structure of long antennae, which he attributed to the deep-sea mode of life. Vanhöffen's comments are important, because although *Microprotus* does not belong to his family "Jolellidae," his family concept clearly indicates that certain of the deep-sea "Janiridae," *Iolella* at least, may need to be recognized as belonging to a separate family with its name corrected to Iolellidae.

Acknowledgments

This paper had its inception when Kussakin asked Wilson to examine *Microprotus caecus* to clarify its relationships with the new species collected during Russian expeditions that are described in this paper. We would like to thank Dr. Thomas E. Bowman, National Museum of Natural History, for loaning the type material of *Microprotus caecus,* carefully reading the manuscript, and offering suggestions for its improvement. We are also grateful to Dr. Boris Mezhov, Zoological Museum of the University of Moscow, for giving us an opportunity to observe *Storthyngura paradoxa* specimens identified by him. This research was partially supported by National Science Foundation Systematic Biology Grants BSR 82-15942 and BSR 86-04573 to Wilson.

Literature Cited

Birstein, Ya. A. 1957. Certain peculiarities of the ultra-abyssal fauna with the example of the genus *Storthyngura.*—Zoologicheskii Zhurnal, 36(7):961–985.

———. 1970. Additions to the fauna of Isopods (Crustacea, Isopoda) of the Kurile-Kamchatka Trench. Part I. *In* Fauna of the Kurile-Kamchatka Trench and its environment.—Akademiya Nauk CCCP, Trudy Instituta Okeanologii Im. P. P. Schirshova 86:292–340. (In Russian, English Translation: Israel Program for Scientific Translations, Jerusalem, 1972)

Haugsness, J. A., & R. R. Hessler. 1979. A revision of the subfamily Syneurycopinae (Isopoda: Asellota: Eurycopidae) with a new genus and species (*Bellibos buzwilsoni*).—Transactions of the San Diego Society of Natural History 19(10): 121–151.

George, R. Y., & R. J. Menzies. 1968a. Species of *Storthyngura* (Isopoda) from the antarctic with descriptions of six new species.—Crustaceana 14(3):275–301.

———, & ———. 1968b. Distribution and probable origin of the deep-sea isopod genus *Storthyngura.*—Crustaceana 15(2):171–187.

Richardson, H. 1910. Isopods collected in the Northwest Pacific by the U.S. Bureau of Fisheries steamer 'Albatross' in 1906.—Proceedings of the United States National Museum 37(1701):75–129.

Vanhöffen, E. 1914. Die Isopoden der Deutschen Südpolar-Expedition 1901–1903.—Deutschen Südpolar-Expedition 15 Zoology, 7:447–598.

Wilson, G. 1989. Deep-sea Lipomerinae and the Munnopsidae (Crustacea: Isopoda: Asellota): a systematic revision.—Bulletin of the Scripps Institution of Oceanography 27:i–xiii, 1–138.

Wolff, T. 1962. The systematics and biology of bathyal and abyssal Isopoda Asellota.—Galathea Report 6:1–320.

(GDFW) A-002, Scripps Institution of Oceanography, La Jolla, California 92093, USA; (OGK & GSV) Institute of Marine Biology, Far East Science Center, Academy of Sciences of the USSR, Vladivostok 690022, USSR.